ESTIMATING POTENTIAL FOR ADAPTATION OF CORALS TO CLIMATE WARMING

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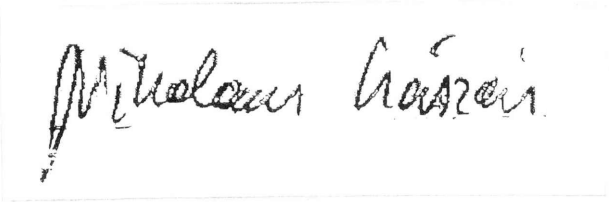
CERTIFICATE OF AUTORSHIP/ORIGINALITY

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.



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ABSTRACT

Climate models predict rapidly warming oceans throughout the 21st century along with increased mortalities in reef-building coral-algal symbioses. Yet the ability of corals to adapt genetically in an evolutionary sense to a warmer climate is unknown. The adaptive potential of corals can be approximated by the extent to which variation in thermal tolerance is caused by genetic factors (i.e. by the broad-sense heritability, H^2). This thesis investigated H^2 in a total of eleven thermal tolerance traits from two populations of the reef-building coral species *Acropora millepora* in the central Great Barrier Reef, Australia. The first population that was investigated associates with thermo-tolerant algal symbionts of the genus *Symbiodinium* (clade D), and came from Magnetic Island (MI), while the second population from Orpheus Island (OI) associates with the intermediately tolerant *Symbiodinium* type C2. Traits investigated were characteristic of the coral host, the algal symbiont, and the holobiont (whole symbiosis).

The present thesis revealed extensive genetic variation in algal symbiont traits, which, together with short generation times, allows for rapid symbiont adaptation to climate warming. A significant adaptive potential was also found for coral colony growth rates, defined here as a holobiont trait. This is in stark contrast to the coral host, which did not display heritability for the majority of the traits investigated for either population. The coral host with its long generation time has therefore only a low potential to adapt to rapidly warming oceans.

Five of the six thermal tolerance traits yielded significant heritabilities in each of the two symbiont types. In clade D symbionts from MI, the adaptive potential was given for the maximum quantum yield of photosystem II, Fv/Fm, one of the most commonly studied stress parameters in coral biology which indicates the overall health condition of photosystems. The one trait that did not yield a significant heritability in D symbionts was non-photochemical quenching (ΦNPQ) of excess excitation energy. The trait ΦNPQ can be considered as a switch for xanthophyll cycling, a mechanism that protects photosystems through conversion of the pigment diadinoxanthin (DD) into diatoxanthin (DT).

However, D symbionts diverted 50 % of the incoming light energy for the initiation of the xanthophyll cycle (i.e. via ΦNPQ), and the xanthophyll cycle mechanism itself showed significant heritability in either symbiont type. Both symbiont types also displayed significant heritability for another measure of photoprotection, the ability to regulate the pool size of photoprotective xanthophyll pigments (XP) relative to total light-harvesting pigments (LH). Although Fv/Fm did not yield a significant heritability in C2 symbionts from OI, both symbiont types again showed heritability for the effective quantum yield of photosystem II (ΦPSII), and for unregulated energy dissipation (ΦNO).

For traits reflecting the function of the coral host, messenger RNA (mRNA) expression levels of four fundamental genes involved in the oxidative stress response were investigated. These genes code for cellular defences which regulate cellular iron homeostasis (i.e. Ferritin), repair denatured proteins (i.e. the heat shock protein Hsp70), detoxify harmful oxygen radicals (i.e. the mitochondrial enzyme manganese superoxide dismutase MnSOD), and might be involved in the dysfunction of coral cell-adhesion proteins during bleaching via a remodelling of surface receptors in the extra-cellular matrix (i.e. a zinc-metalloprotease, Zn^{2+}-met). Each coral host population, however, showed heritability for expression of just one of those four genes (i.e. MnSOD in the MI population, and Zn^{2+}-met in the OI population), therefore displaying only a limited capacity for evolution of thermal tolerance.

Holobiont growth showed a significant heritability in both coral-algal populations, thus providing the basis for evolutionary adaptation. In the long term, however, this trait might be impaired by ocean acidification, which has a negative impact on coral calcification and, therefore, on holobiont growth rates.

In summary, algal symbionts have short generation times and considerable genetic variation in functional traits, thus allowing for rapid adaptation to higher temperatures. However, adaptive response estimates based on low heritabilities in coral host traits along with the coral's mainly sexual reproduction and long generation time raise concerns about the timely adaptation of the holobiont in the face of rapid climate warming.

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LIST OF ABBREVIATIONS

AIMS	Australian Institute of Marine Science
ANOVA	Analysis of Variance
cDNA	Complementary DNA
DD	Diadinoxanthin (xanthophyll pigment, epoxidised)
DT	Diatoxanthin (photoprotective xanthophyll pigment, de-epoxidised)
DT/(DD+DT)	Xanthophyll cycling activity expressed as molar pigment ratio
ECM	Extra cellular matrix
F	Minimum light-adapted fluorescence
F_o	Minimum dark-adapted fluorescence
Fm	Maximum dark-adapted fluorescence
Fm'	Maximum light-adapted fluorescence
Fv	variable fluorescence yield (=Fm-F_o)
Fv/Fm	Maximum quantum yield of Photosystem II
GBR	Great Barrier Reef
G x E	Genotype by environment
GLM	General Linear Model
GOI	Gene of interest
h^2	Heritability in the narrow sense
H^2	Heritability in the broad sense
Hsp70	Heat shock protein 70
ICG	Internal control gene
I-PAM	Imaging PAM
ITS1	Internal transcribed spacer 1
LED	Light emitting diode
LH	Light-harvesting pigments (chlorophyll *a*, chlorophyll *c2*, peridinin, DD, DT)
MI	Magnetic Island
MMP	Matrix metalloprotease
MnSOD	Manganese superoxide dismutase
mRNA	Messenger RNA

OI	Orpheus Island
PAM	Pulse amplitude modulated
PCR	Polymerase chain reaction
PSII	Photosystem II
qP	Photochemical quenching
qN	Non-photochemical quenching
ΦPSII	Effective quantum yield of PSII
ΦNPQ	Regulated non-photochemical energy dissipation (photoprotective)
ΦNO	Unregulated energy dissipation (not photoprotective)
qRT-PCR	Quantitative real-time (or reverse transcription) PCR
R	Response to selection
ROS	Reactive oxygen species
S	Selection differential (strength of selection)
SOD	Superoxide dismutase
SSCP	Single strand conformation polymorphism
SST	Sea surface temperature
T_0	Time-point before the temperature ramp
V_A	Additive genetic variation
V_D	Dominance deviation
V_E	Environmental variation
V_G	Genetic variation
V_I	Interaction deviation
V_P	Phenotypic variation
XP	Xanthophyll pigments (DD and DT)
XP/(LH+XP)	Molar ratio of xanthophyll to total light-harvesting (including xanthophyll) pigments
Zn^{2+}-met	Zinc-metalloprotease

LIST OF FIGURES

this graph represent colonies #2–17 from Figures 5.2–5.5; colonies #17 and #18 shown here represent colonies #19 and #20, respectively. (**A**) Ratio of diatoxanthin to diadinoxanthin (DT/(DD+DT)), (**B**) Ratio of xanthophyll pigments to total light-harvesting pigments (XP/(LH+XP)). Error bars represent standard errors (n=4).

Fig. 5.8 Percent change in expression patterns of four coral stress genes after exposure to bleaching temperature. Note that there is no data for colonies #1 and 18 in bleached samples (explanation in the text), thus colonies #1–16 as shown in this graph represent colonies #2–17 from Figures 5.2–5.5; colonies #17 and #18 shown here represent colonies #19 and #20, respectively. (**A**) Ferritin, (**B**) Hsp70, (**C**) MnSOD, (**D**) Zn^{2+}-met. Error bars represent standard errors (n=4). Note the different scale on the y-axes.

Fig. 5.9 Holobiont growth rates for each of the 20 *A. millepora* colonies (defined as percent change in total coral weight) during 9 days of exposure to bleaching temperature. Error bars represent standard errors (n=4). Note that for the 32 °C treatment, data is missing for colony #1 and #18.

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